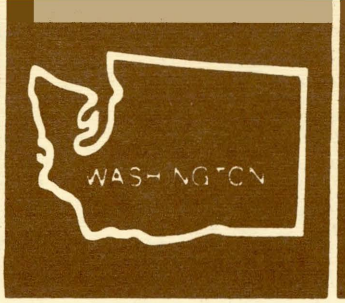

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EFFECTS OF SEMISTARVATION DURING LATE LARVAL STAGES ON SURVIVAL AND FECUNDITY OF THE HEMLOCK SAWFLY IN THE LABORATORY

by

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ABSTRACT

Laboratory feeding tests indicate that hemlock sawfly populations are partially regulated by food quality. Semi-starvation of late-instar larvae, due to feeding on current year's foliage rather than on the normal diet of previous year's foliage, caused a 65-percent reduction in survival of females versus 10 percent in males and a 26-percent reduction in fecundity of surviving females. This selective effect on females may account for the sawfly's apparent inability to reach outbreak proportions comparable to those of such lepidopterous defoliators as the black-headed budworm in coastal Alaska.

Keywords: Entomology, larvae, hemlock sawfly, *Neodiprion tsugae*, western hemlock, *Tsuga heterophylla*.

INTRODUCTION

Hemlock sawfly, *Neodiprion tsugae* Midd., outbreaks occur sporadically in southeast Alaska. In the past, sawfly populations frequently occurred with black-headed budworm, *Acleris variana* (Fern.), populations, but were considered of secondary importance. Since the 1965 area-wide collapse of budworm populations in southeast Alaska (Schmiege 1966), sawfly populations alone have caused heavy defoliation of western

hemlock, *Tsuga heterophylla* (Raf.) Sarg. These sawfly infestations have been confined to localized areas, however, and did not reach the epidemic status common to previous black-headed budworm populations in southeast Alaska.

As with many other conifer-feeding sawflies (MacAloney and Schmiege 1962), the hemlock sawfly normally feeds on previous years' foliage. At high population levels, the "old" foliage is depleted before completion of larval development, and late instar larvae are forced to feed on current year's or "new" foliage. When a hemlock sawfly population is high, a decline frequently follows due to some natural cause such as starvation, disease, parasitization, or a combination of such factors.

This experiment shows direct effects of semistarvation on survival and fecundity of the hemlock sawfly during late larval development. It also suggests that semistarvation was a primary cause of some recent sawfly population declines at scattered locations in southeast Alaska.

METHODS

A feeding experiment using 600 predominantly fourth-instar sawfly larvae was performed under laboratory conditions of 60° F., 75- to 80-percent relative humidity, and 16-hour photoperiod. This approximates dry field conditions in late July and early August. Larvae for the test were collected July 24, 1968, from an apparently healthy field population on hemlock foliage. Each was randomly assigned to a treatment to increase chances of similar sex ratios among treatments since larval sex can be determined only by dissection.

Treatment A consisted of feeding larvae normal hemlock foliage; treatment B, feeding larvae current year's foliage only; and treatment C, placing larvae on bare hemlock twigs. Cut ends of sprigs of foliage and twigs were immersed in water. Each treatment was composed of 10 replicates of 20 larvae per 2x5x7-inch clear plastic cage.

Cage contents were examined on alternate days, and foliage was replaced in treatment A and B cages as needed until all larvae had spun cocoons or died. Unfortunately, sex of dead larvae was not determined because differential mortality of the sexes was not anticipated. Cocoons were placed individually in gelatin capsules until adult sawflies emerged. Females were dissected, and the total number of eggs per female was recorded. Remaining cocoons were dissected and their contents recorded.

Originally, the data were to receive an analysis of variance. However, 14 male adults from treatment A and five male adults from treatment B were used in a sex attractant test and recorded only as to treatment but not by cage number. Therefore, contingency tables were constructed, and chi-square analyses were made to test for significant effects of treatments A and B on overall survival, adult sex ratio, and fecundity. Treatment C was not included in these analyses because complete defoliation of the host has not been observed under natural conditions, and because there were too few female survivors in the treatment to test for differences in fecundity. In addition, bare twigs were not replaced during the test whereas foliage in the other treatments was.

RESULTS

Feeding

Larvae fed mostly on previous years' foliage in treatment A. In treatment B, however, they fed in varying degrees of intensity on "new" foliage, the only food available. Some larvae fed on the bare twigs in treatment C.

Survival

Sawfly survival was lowest under the most stringent feeding conditions of treatment C and the next lowest as a result of treatment B (table 1). Significantly fewer sawflies survived treatment B than treatment A ($\chi^2 = 12.28$, d.f. = 1, $p < 0.005$); therefore, the hypothesis that these two treatments had equal effect on larval survival was rejected. Although some mortality occurred after cocoons were formed, it was not significantly different between treatments ($\chi^2 = 0.57$, d.f. = 1, $p > 0.25$); therefore, the hypothesis that treatments A and B had an equal effect on subsequent mortality was accepted.

Table 1.--*Survival of hemlock sawflies by feeding treatment of late-instar larvae*

Treatment	Test larvae	Dead larvae	Escaped larvae	Cocoons formed	Adult survivors		
					Male	Female	Total
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(A) Normal foliage	200	37	25	138	70	31	101
(B) Current year's foliage	200	66	28	106	63	11	74
(C) Bare twigs	200	114	20	66	44	2	46

A more striking result was the differential effect of feeding treatment on the sexes (table 1, fig. 1). As intensity of starvation increased, significantly fewer females survived ($\chi^2 = 5.93$, d.f. = 1, $p < 0.025$); therefore, the hypothesis that treatments A and B had an equal effect on male and female larvae was rejected. Feeding on bare twigs affected both male and female survival, and most larval mortality occurred within the first week of the test (fig. 2). Feeding only on "new" foliage had little effect on male survival but affected late-developing larvae (fig. 2) which were mostly females (fig. 3). Since male larvae have one less instar than females, they completed development sooner (Hard and Schmiege 1968) and spun cocoons earlier (fig. 3). To illustrate, in each treatment over 75 percent of male survivors emerged from cocoons formed between July 26 and August 2. In each of treatments A and B, more than 80 percent of female survivors emerged from cocoons formed between August 2 and 19. Therefore, males were less subject to effects of semistarvation.

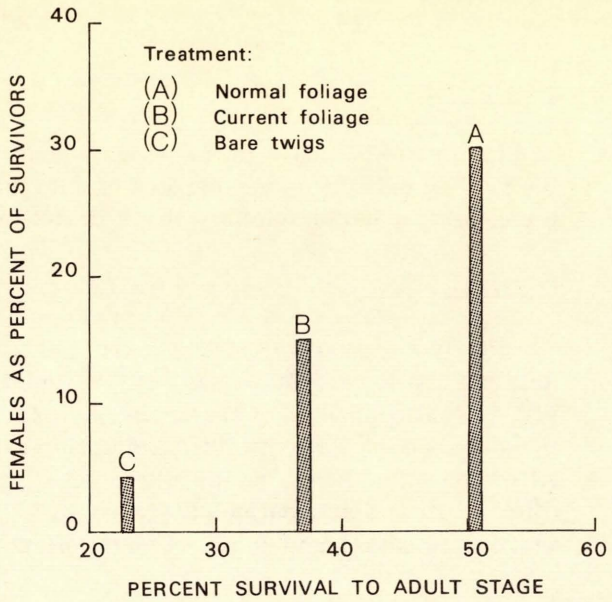

Figure 1.--Relationship between survival of females and survival of both sexes.

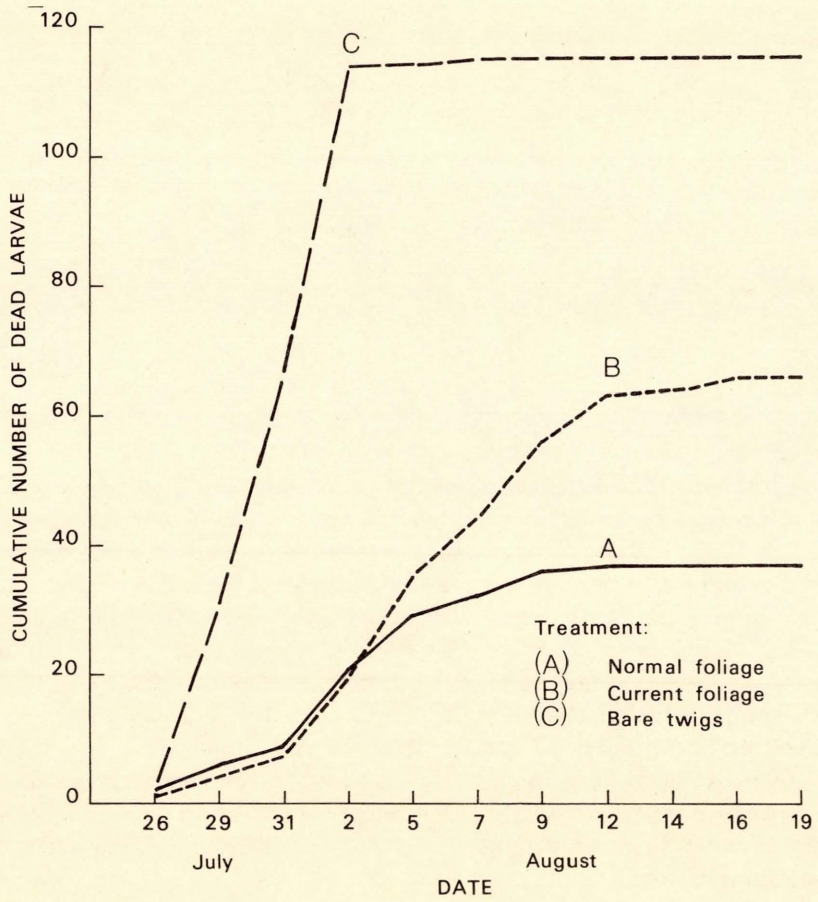

Figure 2.--Cumulative larval mortality by feeding treatment and date.

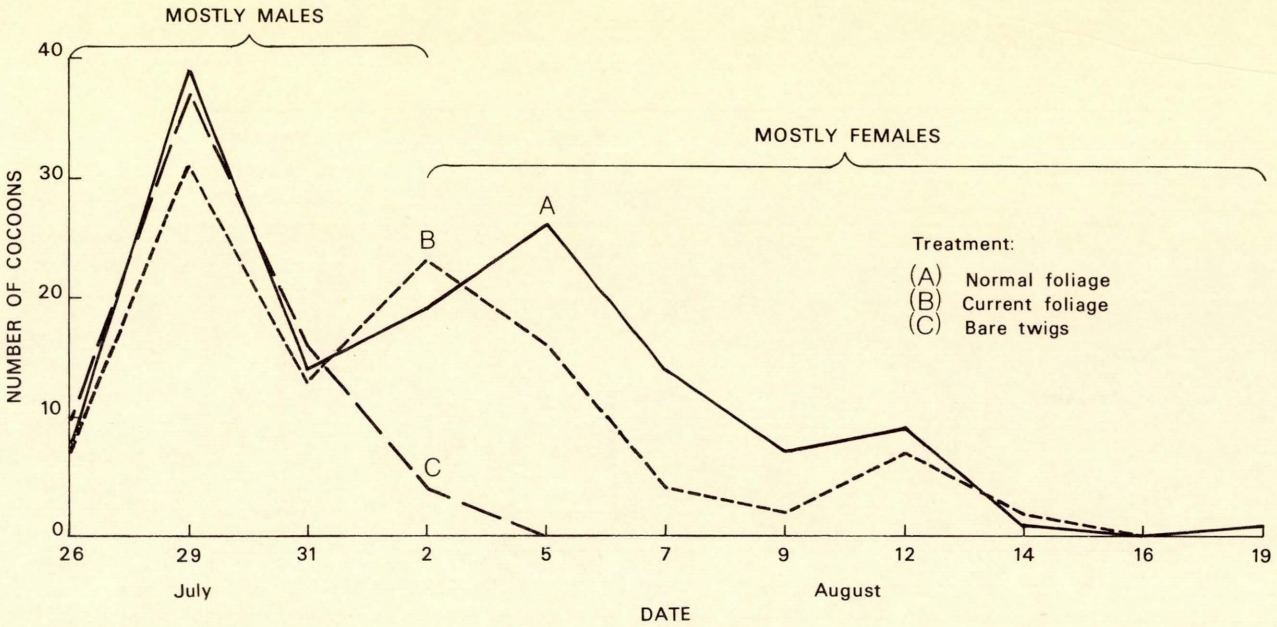

Figure 3.--Cocoon formation by feeding treatment and date.

Crowding stress may have had some effect on larval survival but was apparently not as critical as food quality because the sawfly is a gregarious feeder, although less so in the late instars, and because equal numbers of larvae were placed in the rearing cages.

Fecundity

Of the 44 females that survived the experiment, nine contained dark, free-floating abdominal cysts. These nine (plus two females that escaped) were not included in the egg counts because cysted females are suspected to have a lower than normal fecundity (Sullivan and Wallace 1968). For example, 36 "normal" females from a subsample of 50 additional females contained a mean of 46.19 S.E. ± 2.20 eggs. For the remaining 14 females containing cysts, the mean was 27.79 S.E. ± 3.10 eggs.

The 23 uncysted female survivors of treatment A produced a mean of 50.83 S.E. ± 3.21 eggs, and the 10 uncysted female survivors from treatments B and C produced a mean of 37.30 S.E. ± 2.48 eggs (table 2). The hypothesis that female survivors of treatments A and B had equal fecundities was rejected ($\chi^2 = 21.7$, d.f. = 1, $\rho < 0.005$). These fecundities are lower than those of healthy field populations (Hard and Schmiege 1968), but relative differences due to like feeding conditions in the field are probably similar. Therefore, it appears that semistarvation of females during the last larval instar can cause a significant reduction in egg production. This is to be expected, since insects feed most heavily during the final instar when most egg substrate is produced (Harcourt and Leroux 1967).

Table 2.--*Effects of diet of late-instar larvae on fecundity of the hemlock sawfly*

Treatment	Females	Eggs produced per female	Range of eggs per female
		Number	
(A) Normal foliage	23	50.83 S.E. ± 3.21	17-77
(B) Current year's foliage	8	37.63	26-50
		37.30 S.E. ± 2.48	
(C) Bare twigs	2	36.00	29-43

DISCUSSION

Since the summer of 1966, heavy sawfly populations have been observed at Crab Bay and Todd on Chichagof Island, Jamestown Bay near Sitka, and Irish Creek on Kupreanof Island (fig. 4). In all cases trees were heavily defoliated including current year's foliage.

Although the populations collapsed shortly after discovery, exact causes for the declines were not known. Disease and parasitization were proposed as primary causes, but only limited evidence supported these theories. This study suggests that semistarvation of larvae due to depletion of their natural diet of "old" foliage and forced feeding on "new" foliage, a nutritionally inferior substitute, was the primary cause of population decline.

Larval mortality, due directly to starvation in some areas, could have been increased by death of weakened larvae that succumbed to latent disease. Larval mortality would have little adverse effect on sawfly parasites, since all major hemlock sawfly parasite species in southeast Alaska attack after the sawfly larvae have spun cocoons (Torgersen 1969).

Instead, percent parasitization would probably be magnified because of fewer hosts. This situation could have led to a false assumption that disease, parasitization, or both were primary causes of population collapse, whereas semistarvation of larvae may have predisposed the remaining population to high parasitization and disease. Heron (1955) reported effects of starvation on late-instar larch sawfly larvae in Canada. He did not show differential mortality of the sexes, because males are rare in that species, but did show its effect on larval survival and adult fecundity. Similarly, food shortage in late developmental stages of *Tortrix viridana* Linnaeus in Europe causes desertion of the host, more male than female survivors, and reduced fecundity (Schütte 1957).

Reconstruction of events during a hemlock sawfly population collapse at Taku Harbor revealed the following pattern. Despite heavy defoliation in 1964, noticeably fewer cocoons

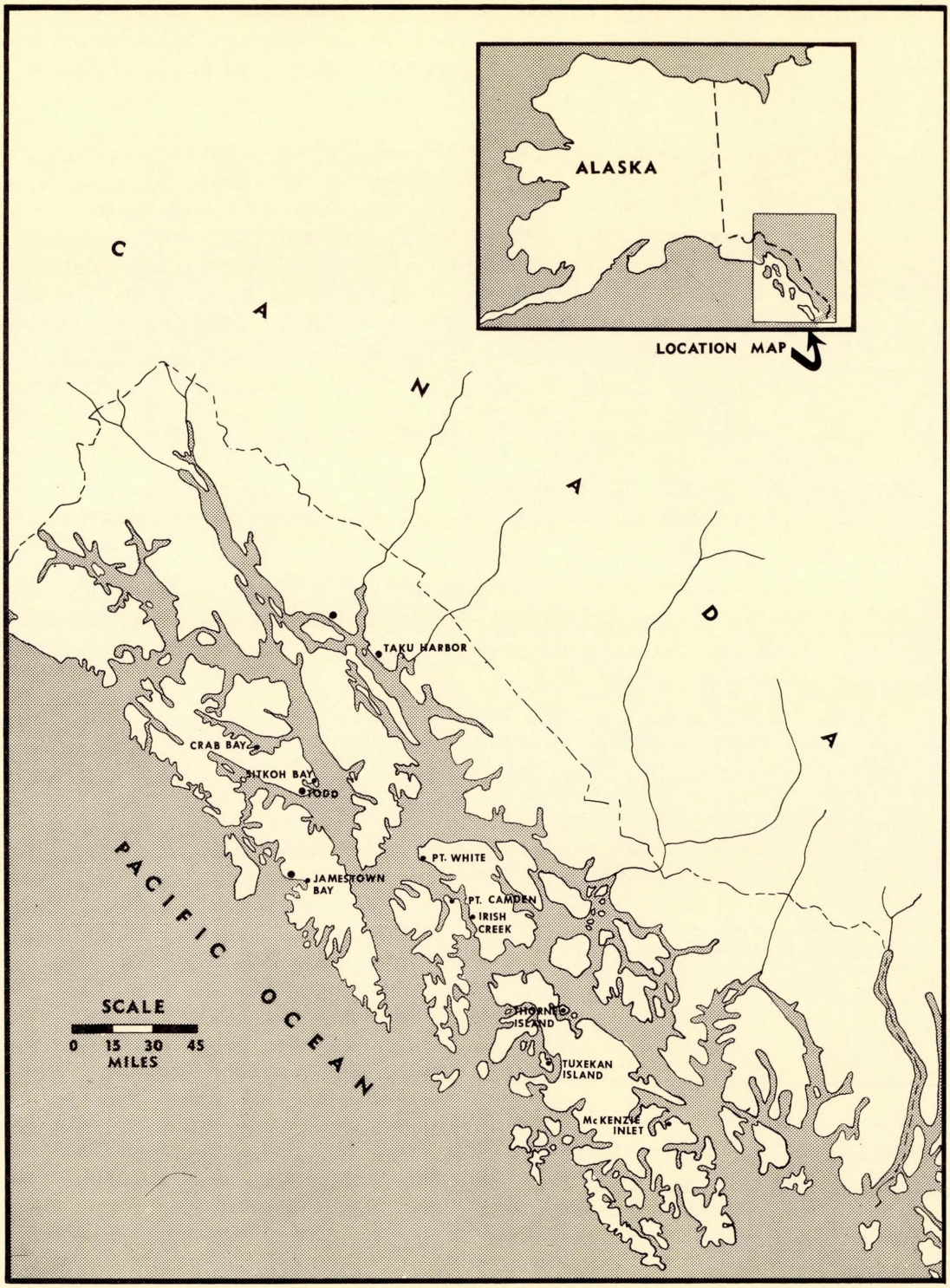

Figure 4.--Southeast Alaska.

were formed than in 1963. Thirty-nine sawflies emerged from a 1964 field sample of 165 cocoons, but only 11 were females. In addition, these females produced a mean of 49.4 S.E. ± 4.0 eggs, whereas 81 females collected in 1963 produced a mean of 72.3 S.E. ± 1.9 eggs.

Semistarvation apparently causes a large reduction in numbers of emerging hemlock sawflies, especially females, and lowered fecundity. This leads to the conclusion that food is an important factor in natural regulation of hemlock sawfly populations and may be primarily responsible for relatively low sawfly population levels in southeast Alaska as compared with budworm population levels. Such a regulatory mechanism would cause a reduction in percentage of females surviving the larval stage, a reduction in fecundity of survivors, and enhancement of subsequent mortality factors such as parasites and disease that attack late in the development of this species.

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